

A name for the clade formed by owlet-nightjars, swifts and hummingbirds (Aves)

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Abstract

Recent phylogenetic studies of non-passerine birds provide congruent support for a clade formed by owlet-nightjars (Aegothelidae) and swifts and hummingbirds (Apodiformes). This clade is here named Daedalornithes (new clade name) based on the principles of phylogenetic taxonomy.

Key words: Daedalornithes, Aegothelidae, Apodiformes, phylogenetic taxonomy

Introduction

The relationships of the swifts and hummingbirds (Apodiformes) to other birds have been a matter of debate, although a close relationship with the nightjars and allies (Caprimulgiformes) has received support from many ornithologists (see Sibley & Ahlquist 1990). Monophyly of Apodiformes is documented by numerous studies (e.g., Cracraft 1988; Sibley & Ahlquist 1990; Bleiweiss *et al.* 1994; van Tuinen *et al.* 2000; Johansson *et al.* 2001; Livezey & Zusi 2001; Mayr 2002; Mayr *et al.* 2003; Chubb 2004). In contrast, monophyly of Caprimulgiformes has not been well-supported. Traits which have been listed as characteristic of Caprimulgiformes, such as a soft plumage, weak feet, and a broad gape (e.g. Bock 1982), may be primitive or may have evolved independently in different groups as adaptations to a similar (nocturnal, aerial and insect-feeding) life-style.

In recent years, various morphological and molecular studies have indicated that Caprimulgiformes is not monophyletic (Johansson *et al.* 2001; Livezey & Zusi 2001; Mayr 2002; Mayr & Clarke 2003; Mayr *et al.* 2003; Chubb 2004; Cracraft *et al.* 2004; Fidler *et al.* 2004). These studies suggested different hypotheses of the relationships of the various ‘caprimulgiform’ birds to other neornithine groups. However, almost all studies that included the owlet-nightjars (Aegothelidae) indicate that this group forms the sister-taxon of the swifts and hummingbirds (Apodiformes). The alliance of Aegothelidae with

Apodiformes was first proposed by Mayr (2002) based on an analysis of 25 morphological characters of eight ingroup taxa. His data set supported a sister-group relationship of Aegothelidae and Apodiformes with 95% bootstrap support. A follow-up study (Mayr *et al.* 2003) included an expanded morphological data set (89 characters, 32 taxa) and also presented molecular sequence data based on three different nuclear genes (*c-myc*, RAG-1, myoglobin intron II; a total of 3254 base pairs). The sister-group relationship of Aegothelidae and Apodiformes was supported by both data sets and in combined analyses (bootstrap support or posterior probability values ranging from 81% to 100%). Three unpublished studies included in Cracraft *et al.* (2004) also supported a sister-group relationship between Aegothelidae and Apodiformes. These include a study of 1100 base pairs of the nuclear gene *c-myc* in 170 taxa (Harshman, Braun & Huddleston), a combined study of 1152 base pairs of the RAG-2 gene and 166 morphological characters (Cracraft, Schikler, Feinstein, Beresford & Dyke), and a study based on a combination of *c-myc* and RAG-2 sequences (Harshman, Braun & Cracraft). A morphological study by Livezey & Zusi (2001) supported a close relationship between Aegothelidae and Apodiformes but placed Caprimulgidae as the sister-group of Apodiformes, and placed Aegothelidae as their sister-group. The study was considered to be preliminary by the authors.

The congruence among morphological and molecular data from several different genes strongly indicates that the sister-group relationship between the owlet-nightjars and the swifts and hummingbirds is not caused by chance but reflects their historical relationships. The clade is supported by multiple, independent lines of evidence and is one of the largest well-supported clades of non-passerines (438 species; cf Dickinson 2003). Formal taxonomic recognition is therefore appropriate. I propose to name this clade:

Daedalornithes, new clade name

Definition: The name Daedalornithes, as defined here, refers to the least inclusive clade comprising *Aegothelus cristatus* (White) and *Apus apus* (Linnaeus). *Aegothelus cristatus* and *Apus apus* are selected as reference taxa because these are the type species of *Aegothelus* and *Apus*, respectively, on which the names Aegothelidae, and Apodidae and Apodiformes, respectively, are based. The definition is based on the principles of phylogenetic taxonomy (de Queiroz & Gauthier 1992). Use of two reference taxa, an owlet-nightjar and a swift, guarantees that the name always refers to a monophyletic group that minimally includes *Aegothelus* owlet-nightjars and *Apus* swifts. Because the definition refers to the least inclusive (i.e. smallest) monophyletic group specified by these two taxa, it excludes all taxa that are placed outside this clade. A node- rather than a stem-based definition of Daedalornithes is selected because its sister-taxon is not resolved (see below), as recommended by Sereno (1999).

Description: Mayr (2002) identified six morphological synapomorphies of Daedalornithes: (i) os palatinum with greatly protruding angulus caudolateralis; (ii) processus

basipterygoidei reduced; (iii) pneumatic foramina on the caudal surface of the processus oticus; (iv) extremitas omalis of coracoid hooked and processus lateralis greatly reduced; (v) musculus splenius capitis with cruciform origin; (vi) caeca absent. Mayr et al. (2003) identified two additional morphological synapomorphies: (vii) processus terminalis ischii of pelvis very narrow and slender, touching pubis at an angle of 45–90°, fenestra ischiopubica very wide; (viii) musculus fibularis longus absent. They identified character (v) as an unambiguous synapomorphy and characters (iii), (iv) and (vi) to (viii) as synapomorphies that, although not unique to Daedalornithes, are optimized in their phylogenetic analysis as independently derived in the common ancestor of this clade.

Taxonomic content: Based on current knowledge (Mayr 2002; Mayr et al. 2003; Cracraft et al. 2004), the name Daedalornithes refers to a clade that, among extant taxa, only includes Aegothelidae (owlet-nightjars), Hemiprocnidae (tree swifts), Apodidae (swifts) and Trochilidae (hummingbirds).

The extinct *Scaniacycspelus*, *Jungornis*, *Argornis* and *Parargornis* are not currently regarded as (crown-group) members of Aegothelidae, Hemiprocnidae, Apodidae or Trochilidae but are part of Daedalornithes based on phylogenetic analysis or the possession of shared derived characters (see Mayr & Manegold 2002; Mayr 2003a, 2003b). The position of the extinct *Aegialornis* and *Eocypselus* relative to Aegothelidae, Apodiformes and Podargidae and, hence their inclusion in Daedalornithes, is unresolved (Mayr 2003a). Two other extinct taxa, *Laputavis* and *Primapus*, were included in Apodiformes by Dyke (2001) but the relationships suggested in this study are considered to be doubtful due to problems with character coding (Mayr 2001).

Phylogenetic relationships: The relationships of Daedalornithes with other birds are as yet unresolved. A morphological study (Mayr 2002) suggested that Daedalornithes is the sister-group of (Nyctibiidae + Caprimulgidae). This study included only eight ingroup taxa and was therefore not designed to exclude other taxa as potential sister-groups of Daedalornithes. Analysis of an expanded data set (Mayr et al. 2003) also identified (Nyctibiidae + Caprimulgidae) as the sister taxon of Daedalornithes but bootstrap support for this grouping was less than 50%. Maximum Parsimony analysis of DNA sequences of three nuclear genes placed Daedalornithes in an unresolved polytomy with Passeriformes and numerous non-passereine groups. Bayesian analysis of the same molecular data set identified Podargidae as the sister taxon of Daedalornithes but with low posterior probability (58%). Combined analysis of morphological and molecular data sets placed Daedalornithes in an unresolved trichotomy with Nyctibiidae and Caprimulgidae, again with low support (50%). A study based on the nuclear gene c-myc (Harshman, Braun & Huddleston in Cracraft et al. 2004) suggested that Trogonidae is the sister-group of Daedalornithes but bootstrap support was not indicated. Two other studies (summarized in Cracraft et al. 2004) could not resolve the sister-group of Daedalornithes. Daedalornithes is therefore best considered as incertae sedis among the ‘higher land bird’ assemblage.

Taxonomic sequence: Due to the unresolved relationships among ‘higher land birds’,

no changes are warranted in the position of Daedalornithes in linear sequences. Thus, I suggest that Daedalornithes is listed after Steatornithidae, Nyctibiidae and Caprimulgidae (cf Dickinson 2003). To reflect their phylogenetic relationships, the taxa included in Daedalornithes are best arranged in the following sequence: Aegothelidae, Hemiprocnidae, Apodidae, Trochilidae.

Etymology: The clade is named after Daedalus, the Greek mythological figure who fabricated wings and improved these until these allowed him and his son Icarus to soar upwards into the air. The name is appropriate in view of the great flight capabilities that evolved within the clade.

Discussion

This paper introduces a new name for a recently-discovered clade. An alternative approach would have been to include Aegothelidae with the swifts and hummingbirds under the name Apodiformes. I have deliberately refrained from doing so because this would result in a change in the meaning of the name Apodiformes which has been almost universally applied to the swifts and hummingbirds (e.g., Wetmore 1951, 1960; Storer 1960, 1971; Bock 1982; del Hoyo *et al.* 1999; Dickinson 2003). Furthermore, if Apodiformes would be expanded to include Aegothelidae, then another name must be adopted for the clade formed by swifts and hummingbirds. Such changes in the use of established names run counter to the principle of stability in zoological nomenclature and are therefore best avoided.

Two other possible names for the clade formed by owlet-nightjars, swifts and hummingbirds are also problematic:

‘Cypselomorphae’— The name ‘Cypselomorphae’ was coined by Huxley (1867) for a group corresponding to Nyctibiidae, Caprimulgidae, Aegothelidae and Apodiformes. Mayr (2002) revived the name ‘Cypselomorphae’ because his morphological analysis indicated that the taxa that were included under this name by Huxley (1867) form a monophyletic group. Thus, both Huxley and Mayr applied the name ‘Cypselomorphae’ to a more inclusive group of taxa than Daedalornithes. For this reason, use of the name ‘Cypselomorphae’ for the clade formed by owlet-nightjars, swifts and hummingbirds would be inappropriate.

‘Apodimorphae’— In their classification, Sibley *et al.* (1988) treated the swifts and hummingbirds at a higher rank than previous taxonomies and applied different names to taxa of which the names were long stable. Thus, Sibley & Ahlquist (1990) used the name Apodiformes for the swifts only, rather than for the swifts and hummingbirds, and introduced the name ‘Apodimorphae’ for the clade formed by swifts and hummingbirds, which since the 1940s were universally called Apodiformes. ‘Apodimorphae’ (sensu Sibley *et al.*

1988) therefore should be treated as a junior synonym of Apodiformes. Sibley & Ahlquist's (1990) DNA-DNA hybridization data on the relationships of swifts and hummingbirds were fully consistent with traditional taxonomies and their proposed taxonomic changes were therefore unnecessary. Re-use of the name 'Apodimorphae' for the clade formed by owl-nightjars, swifts, and hummingbirds is not desirable because it would refer to a more inclusive taxon than to which Sibley *et al.* (1988) applied the name.

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